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A remarkable collection of Late Pleistocene reindeer (*Rangifer tarandus*) remains from Woerden (The Netherlands)

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ABSTRACT

Woerden, in the central part of The Netherlands, is a locality where the amateur-archaeologist Pieter Stoel collected several thousands of fossil mammalian remains of Pleistocene age. The stratigraphically-mixed assemblage includes a broad variety of taxa including species that are indicative of interglacial conditions such as *Hippopotamus* sp. as well as species that inhabited the area during glacial episodes e.g. *Mammuthus primigenius* and *Coelodonta antiquitatis*. The fossil remains have an early Middle Pleistocene – Late Pleistocene age. *Rangifer tarandus* is one of the species that is very well represented in the faunal assemblage from Woerden.

Woerden yielded not only thousands of fossil bones but also Palaeolithic artefacts. A direct relationship between the reindeer bones and these artefacts could not be indicated. Most of the bones are complete and not a single reindeer bone or bone fragment shows traces of human interference such as clear impact or cut marks. This is remarkable considering the many European Palaeolithic sites where reindeer hunters left their traces.

Detailed investigation of the reindeer remains indicates that the majority of the reindeer remains from Woerden represent one population with juvenile as well as adult individuals. The adult specimens show a female/male ratio of 2:1, which is characteristic for natural living reindeer populations. This ratio as well as the standard deviation of the size measurements suggests that the assemblage is one distinct population and not a mix of fossil assemblages with reindeer of different size and different geological ages. Further remarkable is that the dimensions of the limb bones indicate that the reindeer from Woerden were extremely slender; much more slender than the fossil Middle and Late Pleistocene reindeer assemblages from other localities in north-western and central Europe.

1. Introduction

Most of the Dutch Quaternary fossils in the depots of museums, institutes and the large number of private collections of amateur palaeontologists are either from the bottom of the North Sea, the Schelde Estuary, or from a large number of localities inland where sand and gravel, mainly of Holocene and Pleistocene age, are dredged for commercial purposes (Van Kolfschoten, 2001). These localities are often known for their large numbers of mammalian fossils. The fossils are out of context when collected and the assemblages from these localities as well as from the North Sea are often mixed: Holocene, Late Pleistocene and even Early Pleistocene fossil remains might be found together (Van Kolfschoten, 2001).

Woerden, in the central part of The Netherlands, is one of these localities where the amateur-archaeologist Pieter Stoel collected a.o. Paleolithic artefacts as well as several thousands of fossil mammalian remains of Pleistocene age. The mixed assemblage includes a variety of taxa: Carnivora, *Mammuthus primigenius*, *Elephas antiquus*, *Equus* sp., *Coelodonta antiquitatis*, *Stephanorhinus* sp., *Hippopotamus* sp., *Cervus elaphus*, *Megaloceros giganteus*, *Alces alces*, *Bos primigenius* and *Bison priscus*. *Rangifer tarandus* is one of the species that is very well represented in the faunal assemblage from Woerden. Weinstock

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(2000a, 2000b, 2006) showed that the Late Pleistocene reindeer populations from Central and North western Europe are far from uniform and that the body size of reindeer was subject to geographical variation, which did not remain constant through time (Weinstock, 2000a). In order to compare the reindeer from Woerden with the detailed geographical and stratigraphical pattern established by Weinstock (2000a, 2000b, 2006), the body size of the reindeer from Woerden has been calculated using the so-called 'Variability Size Index' (VSI) method developed by Uerpmann (1979, 1982) and Weinstock (2000a). The elaborated data might give an indication for the age of the reindeer assemblage from Woerden as well as an indication for a relation with one of the geographical groups described by Weinstock (2000a).

2. Woerden

The town of Woerden is located in the central part of The Netherlands about 10 km west of the city of Utrecht (Fig. 1). In a small area east of Woerden, in the polders Snel and Polanen, a commercial company (Ballast Van Oord) is dredging and sieving sand and gravel for commercial purposes. The dredging activities started in 1992. In the period 1992–1998, a smaller area (ZLW I), about 0.3 square kilometer, was exploited and a lake was formed. From 1998 onwards, the activities concentrated on a bordering area (ZLW II) about twice as large as the previous one.

Sediments have been dredged from depths to −36 m. The geological setting of the region was recently well investigated using existing borehole data and new borehole material provided by the dredging company (Busschers and Schokker, 2009). On the basis of the borehole information, from about 10 boreholes (with a depth of >20 m) at the site and about 20 within a distance of less than 5 km, a number of sedimentary units were identified. Holocene age clastic sediments (Unit EC; Echteld Formation) and peat (Unit NI; Nieuwkoop Formation) occur in the upper few meters of the dredging site. The Holocene sequence is underlain by Pleistocene eolian sands and coarse-grained fluvial units. The Holocene clay and peat deposits were removed before the sand and gravel extraction started in the second exploitation area (ZLW II). Hence, in that area only the Pleistocene sediments have been dredged.

The uppermost part of the Pleistocene sequence at the dredging site consists of well-sorted eolian sands that were deposited during the second part of MIS2 (Busschers et al., 2007; Unit BXWI). Below this unit, coarse-grained brownish sands are part of the Kreftenheye Formation (Units KR1 and 2). The base of the units KR1-2 occurs at an average depth of −22 m NAP (Table 1). The sands are correlated to the Rhine sediment units B3 and B4 of Busschers et al.

Fig. 1. Geographical position of Woerden and the areas ZLW I and ZLW II. Background: Google Earth.

(2007). Quartz Optical Stimulated Luminescence dating showed the B3 and B4 units were deposited during MIS3 and the latest phase of MIS4. Below the Kreftenheye Formation, two units were identified that contained sands of a more whitish colour (Units BE1 and 2). The base of the units BE1-2 occurs at an average depth of −36 m NAP (Table 1). Commonly, the base is characterized by a gravelly channel lag deposit. The sands are correlated to the Meuse sediment unit S2 of Busschers et al. (2008). Quartz Optical Stimulated Luminescence dating of the S2 unit gave ages falling in MIS 12-11, although these ages have to be treated with caution since the results of quartz OSL at these age ranges has not yet been validated. The ages do, however, suggest a major time hiatus between deposition of the Beegden and Kreftenheye Formation in this area. Rhine sediments of the Sterksel Formation occur below the Meuse sediments. The Sterksel Formation primarily consists of coarse-grained greyish sands with a clayey admixture. The absence of augite, a volcanic mineral that does occur in high amounts in the younger Urk Formation, shows these sediments were formed before ~450 ka (Boenigk and Frechen, 2006).

The Holocene clay and peat deposits, referred to the Echteld Formation and the Nieuwkoop Formation, were removed before the sand and gravel extraction started in the second exploitation area (ZLW II). Hence, in that area only the Pleistocene sediments have been dredged.

3. The fossil mammalian record

The dredged sediments are subdivided into different fractions, and in particular the large fraction is surprisingly rich in mammalian fossils (Fig. 2). To date, thousands of remains of Quaternary large mammals have been collected by Pieter Stoel. The mammalian fossils were first stored in containers at the site and were later transported to the archaeozoological laboratory of the Faculty of Archaeology, Leiden University for identification and analysis. A number of students studied parts of the Woerden collection in the past 5 years and reported their results in their BA- or MA-theses.

The fossil material is rather well preserved. However, the majority of the material is broken due to taphonomical processes in the past. Although part of the material shows signs of erosion, there are no indications of long-distance fluvial transport. There is also no unambiguous indication of human interference. Obvious cut marks, for instance, are missing, and the fracture patterns as well as the marks on the bone surface could be the result of natural taphonomical processes. Recent fragmentation of skeletal remains and molars of (extra) large mammals (elephant, rhinoceros, hippopotamus a.o.) due to the dredging process and the transport through pipes with a maximum diameter of 30 cm, are also frequently observed. Refitting of the fragments that passed through the pipes, as in the case of a fragmented mandible of a straight-tusked elephant *E. antiquus*, leads sometimes to good results (Fig. 3).

The identification of the mammalian remains from Woerden ZLW II has resulted in the following list of Pleistocene taxa: *Castor fiber*, *Panthera leo spelaea*, *Canis lupus*, *Alopex lagopus*, *Vulpes vulpes*, *Crocuta spelaea*, *Ursus arctos*, *Ursus spelaeus*, *Mammuthus trogontherii*, *Mammuthus primigenius*, *E. antiquus*, *Equus* sp., *Coelodonta antiquitatis*, *Stephanorhinus etruscus*, *Stephanorhinus hemitoechus*, *Hippopotamus* sp., *Sus scrofa*, *Cervus elaphus*, *Megaloceros giganteus*, *Capreolus capreolus*, *Alces alces*, *Rangifer tarandus*, *Bos primigenius* and *Bison priscus*.

Studying fossils collected from dredged sediments has one big disadvantage: the material is often mixed. Materials from different layers and hence, of different ages are found together. Even if one dredges from the lowest part of the lake, it cannot be excluded that material from higher up in the sequence has slid down and is dredged up as well at the same time. Consequently, sediments as well as fossils from Early, Middle and Late Pleistocene levels might be mixed. The list of identified taxa presented above indicates that this is also the case with the fossil mammalian assemblage from Woerden. The assemblage includes species indicative of warm/temperate interglacial conditions such as *E. antiquus, Hippopotamus* sp. and *S. scrofa* as well as inhabitants of the so-called Mammoth Steppe Ecosystem characterizing the glacial episodes e.g. *M. primigenius* and *C. antiquitatis*. Based on the common knowledge of the stratigraphic range of the species, as well as on the characteristics of e.g. the *M. primigenius* molars, it can be stated that the majority of the fauna has a late Middle or Late Pleistocene age. However, there are at least two exceptions: *M. trogontherii* and *S. etruscus* are much older. Both occurred during the early Middle Pleistocene or even the late Early Pleistocene. The *Hippopotamus* sp. remains indicate a very large specimen (possibly *Hippopotamus antiquus* (=*H. major*)) known from e.g. the fauna from Untermassfeld (Germany) (Kahlke, 1997) with a late Early Pleistocene age.

An additional explanation for the mixed occurrence of Early, Middle and Late Pleistocene material is that during deposition of the sediments, reworking from a previous position (a palaeosurface) or from older material (a sediment unit) occurred. Because most sediments were deposited in (active) channel systems of the Rhine-Meuse system that eroded vertically (scour) as well as laterally (migration), this process is regarded as highly likely for the Woerden dredging site.

Table 1
Overview of the encountered lithostratigraphical units, the average and variation in depth of the base of the units, the age (based on OSL-dating) and the correlation with the Marine Isotope Stages (modified after Busschers and Schokker, 2009).

Lithological Unit	Average depth of base of the unit (m NAP)	Variation in depth of base of the unit (m NAP)	Age ka	Correlation with Marine Isotope Stages (MIS)
EC	4	2–6	1–4	MIS 1
NI	6	6–7	6–7	MIS 1
BXWI	9	7–11	11–18	MIS 2
KR1	18	16–20	20–48	MIS 3
KR2	22	20–24	63–45	MIS 3-4
BE1	25	23–30	>370	MIS 11
BE2	36	31–38	>370	MIS 11-12
ST	>40	>40	>475	>MIS 12

4. Reindeer *Rangifer tarandus* Linnaeus, 1758

One of the species that is well represented in the Woerden assemblage is *R. tarandus*. The species is of interest in particular since Weinstock (2000a) showed that the Late Pleistocene reindeer populations from Central and North-western Europe vary in body size.

4.1. Body size

Concerning body size, it is important to realize that this term is used in the sense of body mass, not of body height or length of the body. Therefore, the width and the antero-posterior diameter and not the length of the bones were used, because non-length dimensions of proximal limb elements show higher correlations with body mass than do lengths of distal bones (Scott, 1990). In studies on the changes in body size, the dimensions of the dentition are often not taken into account, although there is a correlation between body size and the size of the dentition. The response of the dentition to the environmental changes is, however, slower and the changes are therefore less obvious.

In order to calculate a unit for body size and to be able to merge the data of the different skeletal elements the “Variability Size

Fig. 2. Pieter Stoel collecting a.o. mammalian fossils from the sorted dredged sediments (Photo Andre Ramcharan).

Index" or VSI has been developed and introduced by Uerpmann (1979, 1982) and used by Weinstock (2000a, 2000b) in his osteometrical study of the late Pleistocene reindeer populations in Central and Western Europe. The main advantage of the "Variability Size Index" or VSI method is that it provides the opportunity to merge the data of a single population and to compare the results with that of other (fossil) populations. To calculate the VSI values the following formula is used:

$$\mathrm{VSI} = \frac{x - m}{2*s}*50$$

The 'x' in the formula is the actual value of a given parameter (for instance the distal breadth of the radius). The 'm' is the mean of the same parameter taken from the standard population and the 's' is the standard deviation of the standard population.

Fig. 3. *Elephas antiquus*. Mandible with dp4 and m1 from Woerden (coll. P. Stoel) (Photo Hans van Essen). Scale bar is 10 cm.

The well-preserved fossil reindeer assemblage from Stellmoor (northern Germany) is used as a standard by Weinstock (2000b). The level with the Ahrensburg culture (the Stellmoor Ahrensburgian layer, SAL) in particular is very rich; in total more than 18,000 reindeer bones and antlers were recovered. It was possible to estimate the degree of sexual dimorphism within the population and also to discover the general demographic pattern of the population. Moreover, it is assumed that the material is from a limited time range and the assemblage is therefore regarded as a single population (Weinstock, 2000a).

When discussing the body size of reindeer, it is important that one realizes that the species shows a clear sexual dimorphism. Males are larger than the females, which results in a bimodal pattern in the graphical projection of body size distribution of a reindeer population. However, there is another important aspect that has to be taken into account. The male/female ratio in living reindeer populations changes dramatically as individuals get older. The ratio is about 1:1 until about the age of 2.5 years. After that age, females become more abundant and their arithmetical dominance is obvious at the age of 4 years when the male/female ratio is about 1:2 (Weinstock, 2000b) (Fig. 4). This phenomenon has an impact on the bimodal distribution of the VSI data of a "normal" population. The number of individuals with a larger body size (the males) is smaller and, hence, their peak in the graphs lower.

4.2. *R. tarandus* material from Woerden

Both Inge van der Jagt and Vasiliki Argiti studied parts of the Woerden collection. Together, they referred 289 specimens to *R. tarandus* (Van der Jagt, 2005; Argiti, 2009), mainly based on the morphological characteristics of the different skeletal elements, in particular the metacarpus and the metatarsus. The reindeer collection includes characteristic antler fragments, 3 mandibles with part of the dentition, isolated premolars, several vertebrae and a large number of postcranial bones. Length and width of the (pre)molars (relevant for comparison with Middle Pleistocene reindeer remains) are presented in Table 2.

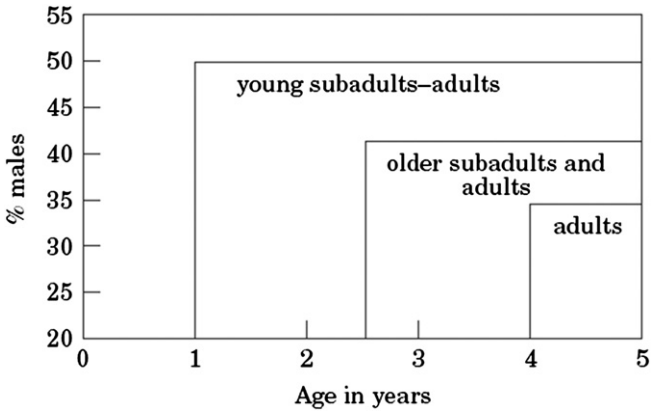

Fig. 4. The frequency of males in the fossil reindeer population from Stellmoor (AL) in the different age-clusters (Weinstock, 2000b).

Almost all (pre)molars are in the first stage of wear. The bones, however, indicate a dominance of adult individuals. Epiphysis and diaphysis are fused in most of the bones. Based on data on the individual age at fusion of epiphysis and diaphysis in the different postcranial elements presented by Hufthammer (1995), it is concluded that about 13.5% of the bones indicate an individual age of less than three years whereas about 28.5% indicate an age of more than three years (Argiti, 2009).

The first collection from Woerden (analyzed by Van der Jagt) contained 109 bones complete enough to allow measurement and the calculation of the VSI values. The values are listed in Table 3. A graphical representation of the data is presented in Fig. 5.

The VSI data most probably indicate a single natural population. Fig. 5 shows a bimodal distribution of the values and also shows that the larger individuals (the right peak, representing the males) are less well represented. Furthermore, the standard deviation of the Woerden material is close to that of populations that have been accepted as a single, natural population (Weinstock, 2000a). The consequence of this conclusion is that the collection studied by Van der Jagt comes from one stratigraphical unit and is not a mixture of reindeer material from different levels.

The analyses show, furthermore, that the mean VSI value of the Woerden assemblage is −57.35 and the mean standard deviation 26.26. If one compares these data with VSI values of other Late Pleistocene reindeer assemblages from Middle and Western Europe presented by Weinstock (2000a) it is remarkable that, in particular, the mean VSI value of the reindeer population from Woerden is very low; lower than the lowest value presented by Weinstock (2000a) in his overview of the VSI values of Late Pleistocene populations from Western and Central Europe. The lowermost mean VSI value he presents is −45.56 for a population from Laugerie Haute (southwest France) with a Magdalenian age. The reindeer from Woerden were apparently extremely slender and hence, had a very low body mass.

Table 2
Rangifer tarandus from Woerden. Length and width of the lower premolars and molars.

(Pre)molars		*N*	x	Min	Max
p2	Length	3	9.6	7.5	11.8
	Width	3	6.4	5.3	6.8
p3	Length	1	14.8		
	Width	1	9.9		
p4	Length	1	15.5		
	Width	1	10.9		
m1	Length	1	16.7		
	Width	1	11.3		
m2	Length	2	25.5	20.2	30.8
	Width	1	9.7		
m3	Length	2	28.9	21.7	36.1
	Width	2	11.6	9	14.1

Table 3
The average VSI values for reindeer measurements from Woerden (Van der Jagt, 2005).

Anat. part	Mean	sd	Max	Min	Number
Sc	−42.48	23.23	−18.92	−71.48	15
Hu	−46.37	27.68	−20.48	−72.26	2
Ra	−58.05	11.81	−31.02	−79.64	14
Ul	−40.66	23.79	−11.56	−59.81	4
Mc	−55.03	21.41	−17.15	−95.65	18
Pe	−56.18	20.75	−24.59	−92.53	8
Fe	−98.41	46.37	−79.8	−142.81	7
Ti	−99.22	45.24	−78.98	−116.02	7
As	−37.79	24.89	−8.84	−77.51	17
Ca	−35.32	27.47	−10.2	−50.51	3
Mt	−61.31	23.07	−17.66	−115.2	14
Total	−57.35	26.26	−8.84	−142.81	109

The osteometrical analysis of a second (more recently collected) assemblage of reindeer material (by Argiti) confirms the conclusions formulated above to a large extent. The VSI values of the 95 bones indicate that the majority of the specimens represent a population with extremely slender individuals. The VSI values of this group also show a bimodal distribution with a mean VSI value of −52.03. However, the second collection also includes 7 specimens that have much higher VSI values, indicating the presence of more robust individuals. These higher VSI values correspond to values known from Late Pleistocene remains e.g. from the North Sea (Van der Leije, 2006). It is assumed that these more robust specimens were dredged from another stratigraphical unit in Woerden.

5. Age of the main reindeer assemblage from Woerden

The occurrence in the fossil record from Woerden of a population of extremely slender reindeer is intriguing. The Late Pleistocene fossil record from Western and Central Europe, investigated in detail by Weinstock (2000a), does not include any population with such low mean VSI values. The Late Pleistocene reindeer from all those sites are more robust. Weinstock, however, analyzed only Late Pleistocene reindeer. This might mean that the Middle Pleistocene reindeer record should be compared to find similar VSI values, an option that should not be excluded as indicated in Table 2.

However, the Middle Pleistocene reindeer record is rather restricted. There are only a few sites where reindeer fossils have been recorded and the number of remains is in most cases rather small. For reliable conclusions on the body size of a particular population it is essential to have insight in the demographic composition of the population. However, the Middle Pleistocene samples which are very small and often exist of fragmented bones are not very suitable for comparison with Late Pleistocene populations.

5.1. Middle Pleistocene record

The oldest reindeer remains known so far are from the early Middle Pleistocene deposits at Süssenborn (Germany). The isolated antler fragments are attributed by Kahlke to *R. tarandus stadelmanni*. "On the basis of the broadly oval cross section of the beams, which have no edges or flattened parts, these antlers are attributed to primitive representatives of the tundra reindeer" (Kahlke, 1999). Worth mentioning is the fact that in Süssenborn, except from the first appearance of reindeer in Europe, the oldest central European musk ox has been found (*Ovibos moschatus suessenbornensis*) (Nilsson, 1983; Kahlke, 2002). Other German localities with an early Middle Pleistocene fauna in which *R. t. stadelmanni* has been

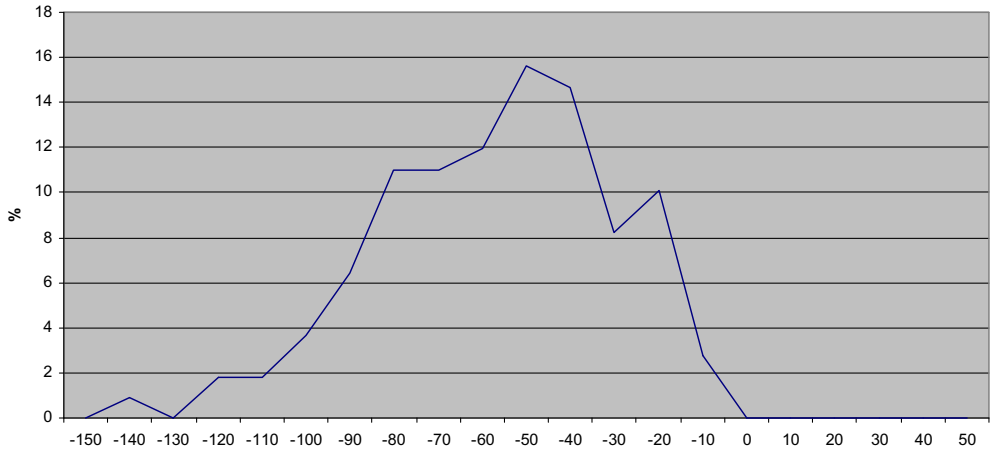

Fig. 5. Distribution of mean VSI values of the fossil reindeer remains from Woerden ($N = 109$) (Van der Jagt, 2005).

recorded are Mosbach and Bad Frankenhausen (Kahlke, 2002). The reindeer fossils have been found in association with species that also inhabited the northern tundra as well as continental steppe biotopes. The associations represent the early Middle Pleistocene "Mammoth Steppe" fauna.

Late Middle Pleistocene reindeer remains were recorded from the German localities Ariendorf (a fragment of an antler), Schweinskopf (Sk3 and Sk4) (premolars, molars and postcranial remains) and Wannen (Wa 3) (postcranial remains) (Turner, 1990). The dimensions of the scarce remains published by Turner (1990) suggest at least that the individuals are more robust than those from Woerden.

The oldest reindeer record from the British Isles is from the early Middle Pleistocene deposits at Westbury-sub-Mendip where an antler fragment attributed to *R. tarandus* was found (Andrews et al., 1999). Reindeer material is known from the Anglian Stage (Elsterian) from the sites of Hall's Pit (near Benson), at Wortwell in Norfolk and at Homersfield in Suffolk. From the Wolstonian stage (Saalian) reindeer material has been found in the Bagington-Lillington Gravels in Warwickshire (Stuart, 1982). The British *Rangifer* remains are found in association with treeless "steppe-tundra" vegetation, but they also occur during the Chelford Interstadial in association with boreal forest.

The French locality Tautavel-Arago, with a Middle Pleistocene age (c. 600–400 ka) with at least 80 individuals is the locality with the most abundant Middle Pleistocene reindeer record. To date, no data on the dimensions of the reindeer from Tautavel-Arago have been published. The analyses using the VSI method are in progress and the preliminary results (Anne-Marie Moigne personal communication) indicate that the reindeer from Tautavel-Arago is as robust as the one from Stellmoor, the population used as standard by Weinstock in his analyses of the Late Pleistocene populations. Thus the reindeer from Tautavel-Arago also appear to be more robust than those from Woerden.

Other French localities where Middle Pleistocene reindeer with a younger age have been recorded are: Achenheim, La Fage, Chatillon-Saint-Jean, and La Micoque (Layer 3). The locality Combe-Grenal in the Dordogne indicated that the reindeer seems to become abundant at the end of the Middle Pleistocene. In the late Middle Pleistocene fauna from Abri Suard La Chaise it is the most abundant species (Delpech and Heintz, 1976). For the size of reindeer during the Middle and Late Pleistocene there is some general information. Bouchud (1972) did a comparative analysis of the dental measurements of the sites dating to the late Middle Pleistocene (La Fage) and sites dating to the Late Pleistocene (La Chaise), and concluded that the upper and lower third molars with a late Middle Pleistocene age are generally bigger than those from the Late Pleistocene. However, the VSI values of the oldest reindeer remains from Combe-Grenal level 64–61 (referred to MIS 6) have a mean value of −37.41 ($N = 19$) indicating rather slender individuals; those from MIS 6 levels higher up in the sequence Combe-Grenal 60 ($N = 33$), 59 ($N = 96$) and 58 ($N = 28$) have VSI values of respectively −19.72, −15.89 and −1.54 indicating an increase in robustness (Weinstock, 2000a).

R. tarandus has also been recorded from the Iberian Peninsula from the site of La Parte (northern Spain). The record includes molars and fragments of postcranial elements. They are found in association with remnants of *C. antiquitatis*. The fauna has a minimum age of 150 ka and dates most probably to the late Middle Pleistocene (Alvarez-Lao and García-García, 2006). The size of the molars presented by Alvarez-Lao and García-García (2006) indicates rather robust individuals.

Summarizing, *R. tarandus* occurred in Central and Western Europe at least since the early Middle Pleistocene. However, during the Middle Pleistocene the species was generally less abundant compared to the Late Pleistocene. The fauna from Tautavel-Arago as well as the late Middle Pleistocene (MIS 6) faunas from the Dordogne, such as Combe-Grenal, are in this aspect exceptions. The fact that *R. tarandus* is generally rare might indicate that the Middle Pleistocene fossil record mainly involves legacies of winter immigrants from northern or north-eastern regions.

Because the Middle Pleistocene reindeer fossil material is quite sparse and fragmented (combined with the fact that the entire record has not been published in detail), it is not possible to get a complete picture of the variation in body size of the Middle Pleistocene reindeer. The majority of the remains indicate that the Middle Pleistocene reindeer are more robust than those from Woerden. However, the oldest reindeer remains from Combe-Grenal level 64–61 (referred to MIS 6) also have a remarkable low mean VSI value indicating that during the late Middle Pleistocene slender reindeer occurred. Hence, a Middle Pleistocene age of the Woerden slender reindeer assemblage cannot be excluded.

5.2. Late Pleistocene record

The Late Pleistocene record was investigated extensively and described by Weinstock (2000a). His analyses indicate that the Late Pleistocene VSI values are far from identical. There appear to be fluctuations through time as well as geographical differences. The extensive Late Pleistocene record from southwestern France shows large differences in VSI values. The reindeer from the Mousterian fauna of Combe-Grenal level 25–23, referred to MIS 4, has a mean VSI value of −9.16 ($N = 135$) and Combe-Grenal level 19–17, referred to MIS 3, has a mean VSI value of −23.13 ($N = 13$). The localities Laugerie Haute west and Laugerie Haute east yielded

Table 4
VSI values of reindeer remains from Upper Palaeolithic sites Laugerie Haute and Gare de Couze (southwestern France) compared with climatic conditions during time of deposition (based on data from Weinstock, 2000a).

Site/Layer	Period	Age	Mean VSI	Climate as suggested by faunal composition
Laugerie Haute west 12	Lower Solutrian	Lower Solutrian	−25.04	Cold, somewhat humid in later part
Laugerie H. east 20-18	Magdalenian 0	Magd 0	−35.51	Cold and very dry
Laugerie H. east 17-9	Magdalenian I	Magd I	−31.89	Cold, less dry than Magd 0
Laugerie H. east 8-4	Magdalenian II	Magd II	−45.56	Cold and very dry
Laugerie H. east 3-2	Magdalenian III	Magd III	−30.71	Cold and very dry
Gare de Couze G, G0, G1	Magdalenian VI	Magd VI	−17.83	More humid

a large number of Late Pleistocene (MIS 2) reindeer remains ranging in age from 20,750 ± 150 to 13,970 ± 480 BP (Weinstock, 2000a). The mean VSI values of the Laugerie Haute assemblages are rather low (Table 4). The reindeer from La Madeleine and Gare de Couze, which are chronologically younger than those from Laugerie Haute, are more robust.

The increase in VSI values at the end of the Late Pleistocene can also be observed in the fossil record from southern Germany and Switzerland. The reindeer from the Aurignacian and Gravettian sites have mean VSI values of respectively −4.92 and −4.97 whereas Magdalenian reindeer are clearly less robust with mean values ranging from −17.84 to −22.41. Four sites located in northern Germany (Salzgitter-Lebenstedt, Köningsaue, Meiendorf and Stellmoor) yielded larger collections of reindeer material. The fossils from Salzgitter-Lebenstedt date from the early Weichselian, those from the latter two localities from the very late Weichselian. Mean VSI values indicate an increase in robustness between the reindeer from Salzgitter-Lebenstedt (mean VSI value −18.15) and those from Stellmoor (Ahrensburgian Layer; mean VSI value 0.5).

Reindeer bones are also well represented in the chronologically mixed Pleistocene mammalian record from the bottom of the North Sea (Van Kolfschoten and Laban, 1995; Van Kolfschoten and Van Essen, 2004; Glimmerveen et al., 2005). ^{14}C dates of 9 reindeer fossils show a range of 29,460 ± 250 to >45,000 BP. In total, 97 reindeer bones from the North Sea (Brown Bank) region have been measured. The result is a rather uniform VSI value distribution as known from other (non-mixed) localities, a mean VSI value of 5.40 and an SD of 27.30 suggest that we are dealing with a 'normal' population with no extreme variation in robustness despite the fact that the material varies in age (Van der Leije, 2006).

The relevant, elaborated fossil record from the British Isles is restricted to that of three sites: Sandfort Hill, Kent's Cavern and Ossom's Cave. The fauna from Sandfort Hill is correlated with the middle Weichselian (MIS 3); the reindeer have a mean VSI value of −29.45 ($N = 126$) whereas the remains from Kent's Cavern and Ossom's Cave are much younger and date from the very late Weichselian. The mean VSI values of the reindeer from these sites are respectively −7.78 and −6.21 (Weinstock, 2000a).

The Late Pleistocene reindeer record presented above indicates that the robustness is very variable through time and space. A few populations are roughly as robust as the standard population whereas others are very slender although not so extreme as the population from Woerden. Taking into account that knowledge of the Late Pleistocene record is not complete, a Late Pleistocene age for the Woerden assemblage should not be excluded.

5.3. Geographical variation

Looking in particular at the Late Pleistocene record from the different regions, one can observe geographical differences in the abundance and size of the reindeer. Comparing the (late MIS 3 and MIS 2) reindeer record from southwest France with that of southern Germany, one can conclude that for the different periods mentioned above, reindeer are less abundant in southern Germany and more robust. The mean VSI values of the northern German populations are even higher in comparison to those of the southern German VSI values. This is, however, the result of the fact that the females are larger whereas the males have about the same size as their counterparts from southern Germany.

6. Discussion and conclusion

Based on the Middle and Late Pleistocene reindeer data presented above, the slenderness of the reindeer from Woerden is remarkable. The slenderness is not indicative of populations with either a Middle or Late Pleistocene age. The Middle and Late Pleistocene data suggest first of all that the presence of a very slender reindeer population is indicative of periods with cold and very dry climatic conditions. That would imply that the reindeer material from Woerden dates most likely from cold periods during the late Middle Pleistocene (MIS 6) or the late Weichselian (MIS 2). However, low VSI values such as those from Woerden have not been recorded so far for sites dating from these periods. An MIS 6 or MIS 2 age also conflicts with the single ^{14}C date obtained for a mixture of well-preserved reindeer bones. This large sample was dated by a conventional laboratory to 30,280 ± 450 BP (GrN-30858). Calibration using the latest calibration curve intcal09 (Reimer et al., 2009) yields a numerical age range (1-sigma) of 34,550–35,200 calBP.

The ^{14}C age indicates an MIS 3 age, which is a period of rapid and major climatic fluctuations that caused enormous environmental stress (Stringer et al., 2003) that would have had its impact on reindeer populations in Europe. Looking at the factors that influence body size, one can assume that there are at least two scenarios that might explain a population dominated by very slender individuals (Beeren, 2008). The first scenario assumes a high intraspecific competition as a result of an expanding population that lives under favorable climatic conditions. Another scenario is also possible, however. If the winters are harsh, many animals in a population will die, most likely of starvation. The low temperatures in combination with high precipitation cause a high snowfall and ice forming. This greatly diminishes the accessibility of the lichens on which the reindeer feed in winter. The moment of snowmelt has a great influence on the emergence, flowering and reproductive success of northern plants (Post and Stenseth, 1999). Low temperatures and high precipitation could delay the vegetation onset if it continues into spring causing the forage quantity and quality to decrease and thus the growth season to shorten. A late vegetation onset causes females to give birth to calves of a smaller body size. Weladji and Holand (2003) found that females of a low birth mass gave birth to lighter calves which are more prone to early mortality. As a consequence the reindeer would be unable to increase their body growth and thus would remain small. An alternation/combination of the two scenarios within a period of rapid major climatic fluctuation as known from the Middle Weichselian (MIS 3) might have prevented recovery from the poor conditions and thus might have resulted in the extreme decrease in size. This scenario is in accordance with the acquired ^{14}C date. However, more ^{14}C dates are needed to confirm this preliminary conclusion on the age of the

slender Woerden reindeer. This conclusion is, however, difficult to match with known VSI values from that period that are much higher; the robustness of the southern German populations are even close to that of the standard populations. These data question a MIS 3 age.

If one assumes that the MIS 3 age for the reindeer population is correct, this indicates that the reindeer assemblages come from the Kreftenheye Formation unit 1 (KR1) (Table 1). This does, however, not imply that all mammalian fossils are from that unit. As stated above, the Pleistocene mammalian assemblage is mixed; both warm- and cold-adapted species are in the Woerden assemblages. Furthermore, mammals were present not only from Late Pleistocene but also from Middle Pleistocene levels (e.g. *M. trogontherii*). The presence of species from different chronological periods and different climatic conditions and environments suggests that the Woerden material covers a larger period of time.

It is obvious that more research is needed to disentangle the fossil mammalian record from Woerden. Clearly, more ^{14}C dates are needed; even more important is that the original depth of the finds is known. Without such information it is almost impossible to make a distinction between the different natural assemblages present at Woerden and to establish the exact date of the reindeer populations which is needed to get an idea about the significance of the low VSI value of the reindeer. As long as this information is absent, any analysis is a sophisticated guess.

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